NUTRIENT UPTAKE

Temporal Changes in Soil and Biomass Nitrogen for Irrigated Wheat Grown under Free-Air Carbon Dioxide Enrichment (FACE)

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ABSTRACT

Increasing atmospheric CO_2 concentrations are expected to increase plant production and demand for N and other nutrients. The objectives of this investigation were to characterize and quantify the temporal trends in soil mineral N and aboveground biomass N during the growing season of wheat (*Triticum aestivum* L.) with adequate N, ambient and elevated CO_2, and two levels of water stress. The free-air CO_2 enrichment (FACE) technique was used to enrich the air from 370 to 550 μmol mol^{-1} CO_2. Spring wheat was planted in late December of 1992 and 1993 and harvested at the end of May. Each main plot (CO_2 level) was split into two irrigation treatments to replace 100 and 50% of the potential evapotranspiration. Soil and plant samples were taken for N analysis six times each year. Elevated CO_2 lowered soil mineral N concentrations in the top 0.3 m of soil as much as 40% and increased aboveground biomass N by as much as 16% compared with the ambient treatment. Before anthesis, irrigation level had little effect on either soil mineral N or aboveground biomass N, but at harvest in 1992–1993 and at dough stage in 1993–1994 deficit-irrigated plots had higher soil mineral N ($p < 0.05$) and lower aboveground biomass N than plots that received adequate irrigation. There was little variation in the concentrations of N in the aboveground biomass among treatments within a sampling date. The data suggest elevated CO_2 may lead to rapid N uptake, which could result in increased early vegetative growth.

The concentration of atmospheric CO_2, currently ~350 μmol mol^{-1}, is increasing at a rate of 1.5 μmol mol^{-1} yr^{-1} (Watson et al., 1990). A greater CO_2 concentration is expected to increase the production of plant biomass. However, results from experiments on the effects of elevated CO_2 on plant growth vary widely. Plants (C3) increase their biomass by 0 to 37% (Cure and Acock 1986; Pinter et al., 1996) and yields from −40 to +400% (Kimball, 1983) in response to a doubling of the atmospheric CO_2, depending on the conditions of the experiment and the plant used. The large variability in response indicates the importance of the interaction of other environmental factors with CO_2.

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Nitrogen is the plant nutrient most likely to limit plant growth. Research to determine the interactions of nutrients such as N with CO_2 have produced variable results. Crops that are grown with insufficient N and increased CO_2 can sometimes result in lower grain yields (Cure et al., 1988; Goudriaan and de Ruiter, 1983; Israel et al., 1990; Kimball et al., 2002). Even with suboptimal N, there are usually periods before N is depleted in which the CO_2-enriched plants have more vegetative growth than N-deficient plants grown at ambient CO_2 (Cure et al., 1988; Israel et al., 1990; Mitchell et al., 1993). No differences were found in leaf N concentrations of wheat due to varying CO_2 when N levels were not limiting, but when N was limiting, leaf N was decreased when CO_2 was increased (Sinclair et al., 2000). This contradicts in part the general trend of lower N concentrations in vegetative growth when plants are grown under elevated CO_2 than plants grown under ambient conditions (Cotrufo et al., 1998). Mitchell et al. (1993) attributed the lower grain yields of low N wheat plants under high CO_2 to rapid uptake of N during the vegetative growth phase when more N was available. In their experiment, nearly half of the N was applied soon after planting and was available for vegetative growth. The plants were not able to translocate sufficient N from vegetative parts to produce grain. Experiments in which there is a constant supply of N throughout the growth period tend to have both increased biomass and increased grain yield under elevated CO_2 (Mitchell et al., 1993; Cure et al., 1988; Kimball et al., 2002).

Elevated CO_2 may cause significant changes in root morphology (Rogers and Runion, 1994). The root systems of several agronomic species have been shown to respond to increased CO_2 with more massive and branched root systems that occupy greater soil volume than those of plants grown under ambient conditions (Chaudhuri et al., 1990; Del Castillo et al., 1989; Prior et al., 1995; Mitchell et al., 1993; McKee and Woodward, 1994). In a survey of a wide range of free-air CO_2 enrichment experiments, Kimball et al. (2002) reported that belowground development was stimulated more than aboveground development under elevated CO_2. Wechsung et al. (1995, 1999) found that an increase of 180 μmol mol^{-1} of CO_2 produced as much as a 37% increase in root mass as well as increased root depth in wheat.

Abbreviations: DOY, day of year; Dry, water-stress treatment; FACE, free-air carbon dioxide enrichment; GLM, General Linear Model Procedure; MAC, University of Arizona Maricopa Agricultural Center; Wet, well-watered irrigation treatment.

They found that changes in root density and length were present as early as the three leaf stage. Enhanced root growth allows plants grown under elevated CO_2 to take up nutrients and water more rapidly and from a greater soil volume than those grown under ambient CO_2 levels.

While studies have shown that elevated CO_2 levels increase both aboveground and belowground biomass, the effect of elevated CO_2 on the rate of uptake of soil nutrients to support the increased growth rates under field conditions has not been well documented. The objectives of this field study were to characterize and quantify the temporal trends in soil mineral N and aboveground biomass N during the growing season of wheat with adequate N, ambient and elevated CO_2, and two levels of water stress.

MATERIALS AND METHODS

A spring wheat experiment was conducted for 2 yr at the University of Arizona Maricopa Agricultural Center (MAC), Maricopa, AZ. The free-air CO_2 enrichment (FACE) technique was used to enrich the air in circular plots within a wheat field to 550 μmol mol^{-1} CO_2, as done previously in 1990 and 1991 with cotton (*Gossypium hirsutum* L.) (Hendrey, 1993; Hendrey et al., 1993; Wall and Kimball, 1993; Mauney et al., 1994; Dugas and Pinter, 1994). The average ambient CO_2 concentration was 370 μmol mol^{-1} in both years (Kimball et al., 2001). Four replicate 25-m diameter toroidal plenum rings constructed from PVC pipe with a nominal internal diameter of 300 mm were placed in the field shortly after planting. The rings had 2.5-m high vertical pipes with individual valves spaced about every 2 m around the periphery (Wall and Kimball, 1993; Lewin et al., 1994). Air enriched with CO_2 was blown into the rings, and exited through tri-directional jets in the vertical pipes at elevations near the top of the crop canopy. The center-to-center spacing of the rings was 90 m (Wall and Kimball, 1993). Additional information on the operating parameters and performance limitations of the FACE apparatus are described by Hendrey et al. (1993) and Nagy et al. (1994). The FACE treatment was applied continuously from emergence to harvest, except the last 2 wk of January 1993 when enrichment was shortened to 8 h d^{-1} centered about solar noon to conserve the CO_2 supply while heavy rains curtailed CO_2 deliveries.

Each of the main circular FACE and Ambient plots was split into semicircular halves, with each half receiving either a well-watered (Wet) irrigation treatment or a water-stress (Dry) treatment (Wall and Kimball, 1993; Hunsaker et al., 1996). The irrigations were accomplished using a subsurface drip system with a tube depth of about 0.20 m, a tube spacing of 0.50 m, and an emitter spacing of 0.30 m. The Wet plots were irrigated after 30% of the available water in the root zone was depleted. Plots were irrigated with an amount calculated to replace 100% of the potential evapotranspiration since the last irrigation, adjusted for rainfall (Fox et al., 1992). In 1992–1993, the Dry plots were irrigated at the same time as the Wet plots, but they received half as much water. In 1993–1994, to improve uniformity of the water distribution, the Dry plots were irrigated every other time the Wet plots were irrigated but the amounts of the irrigations were similar. Cumulative irrigation totals between emergence and harvest for the Wet treatments were 600 and 620 mm for 1992–1993 and 1993–1994, respectively. For the Dry treatments, irrigation totals were 275 and 257 mm. Cumulative rainfall during the same periods was 76 mm for 1992–1993 and 61 mm for 1993–1994.

In both years of the study, the crop was planted in east–west rows spaced 0.25 m apart (parallel to the drip irrigation tubing). In 1992–1993 wheat was planted on 15 Dec. 1992 with 50% emergence on 1 Jan. 1993, when CO_2 treatments were initiated. In 1993–1994 the crop was planted on 7 to 8 Dec. 1993 with emergence and start of FACE on 28 Dec. 1993. Both crops followed wheat stubble and all rings and treatments were located in the same positions in both years. The soil, which had a pH of 8.5 throughout the profile, was classified as Trix clay loam. Additional details about the soil properties are given by Post et al. (1988) and Kimball et al. (1992). Before planting the soil was rototilled following a pre-irrigation. Immediately after planting the 1992–1993 crop was drip irrigated, whereas the 1993–1994 crop was sprinkler irrigated. The latter strategy permitted the upper part of the soil profile to be wetted enough for germination without also having to fill the lower part of the profile. Therefore, in 1993–1994 a more severe water stress was imposed earlier than was accomplished in 1992–1993. The plant densities in 1992–1993 were 130 plants m^{-2} at emergence and 109 plants m^{-2} at harvest; in 1993–1994 they were 186 plants m^{-2} at emergence and 152 plants m^{-2} at harvest. A combination of biological and chemical methods were used for pest control, with no significant loss of growth or yield. Air temperatures (2.0 m height) ranged from −1.1 to 37.7°C in 1992–1993 and from −4.5 to 39.2°C in 1993–1994. Final harvests of the two crops were on 24 May 1993 and 1 June 1994.

Soil samples were taken from the top 0.3 m of soil in all plots before planting in both years, and the plots were fertilized so that nutrients were nonlimiting. Preplant applications of granular fertilizer supplied 5.4 g N m^{-2} and 2.9 g P m^{-2} in both years. On 30 Jan. 1993, a super-phosphoric acid application supplied an additional 1.5 g P m^{-2} so the total P applied was 4.4 g m^{-2} in 1992–1993 and 2.9 g m^{-2} in 1993–1994. Additional N fertilizer as urea–ammonium nitrate solution 32% N (Uran-32) was applied through drip irrigation tubes at rates of 9.2, 5.9, and 7.2 g N m^{-2} on 30 Jan. 1993 (day of year [DOY] 30), 18 Mar. 1993 (DOY 77), and 5 Apr. 1993 (DOY 95), respectively, so the total amount of N applied to the 1992–1993 crop was 27.7 g N m^{-2}. Similarly Uran-32 was applied at rates of 9.2, 6.9, and 4.6 kg N ha^{-1} on 3 Feb. 1994 (DOY 34), 16 Mar. 1994 (DOY 75), and 8 Apr. 1994 (DOY 98), respectively, so the total N applied to the 1993–1994 crop was 26.1 g N m^{-2}. Postplanting fertilizer applications were based on the N content of stem samples taken 3 to 4 d before the fertilizer applications (Doerge et al., 1991).

Soil samples were taken on DOY 16, 23, 43, 70, 113, and 148, which corresponded to the three-leaf stage, tillering, stem elongation, boot, dough development, and final harvest, respectively, in 1993 and DOY 4, 32, 63, 103, 120, and 150, which corresponded to the three-leaf stage, tillering, stem elongation, early milk, dough development, and final harvest, respectively, in 1994 (Table 1). At the beginning of both seasons there was a period of time in which no differential water treatment had been applied; during those periods, only the Dry plots were sampled. Three soil cores were taken in each plot to a maximum depth of 1.0 m, unless otherwise specified. Sample depths were shallow early in the growing season and increased in depth throughout the season in response to anticipated root development. In 1992–1993, cores were divided into 0.15-m sections from the 0- to 0.60-m soil depth, and 0.20-m sections from the 0.60- to 1.0-m depth. In 1993–1994, cores were divided into 0.15-m sections from the 0- to 0.30-m soil depth, a 0.30-m section from the 0.30- to 0.60-m depth, and into a 0.40-m section from the 0.60- to 1.0-m depth except for the last sampling date in which the 1992–1993 system was used. Samples were stored under refrigeration (4°C) until the samples were processed, usually within 48 h.

Table 1. Soil and plant sampling dates, day of year (DOY), and growth stage for wheat in 1992–1993 and 1993–1994.

1992–1993		1993–1994	
Soil	Plant	Soil	Plant
16 Jan. 1993	12 Jan. 1993	4 Jan. 1994	4 Jan. 1994
DOY 16	DOY 12	DOY 4	DOY 4
Three leaf	three leaf	three leaf	three leaf
23 Jan. 1993	1 Feb. 1993	1 Feb. 1994	25 Jan. 1994
DOY 23	DOY 32	DOY 32	DOY 25
Tillering	tillering	tillering	tillering
12 Feb. 1993	2 Mar. 1993	4 Mar. 1994	8 Mar. 1994
DOY 43	DOY 61	DOY 63	DOY 67
Stem elongation	stem elongation	stem elongation	stem elongation
11 Mar. 1993	31 Mar. 1993	13 Apr. 1994	12 Apr. 1994
DOY 70	DOY 90	DOY 103	DOY 102
Boot	early milk	early milk	early milk
23 Apr. 1993	21 Apr. 1993	30 Apr. 1004	26 Apr. 1994
DOY 113	DOY 111	DOY 120	DOY 116
Dough	dough	dough	dough
28 May 1993	19 May 1993	30 May 1994	25 May 1994
DOY 148	DOY 139	DOY 150	DOY 145
Final harvest	final harvest	final harvest	final harvest

Soil samples were sieved in the field moist condition to pass 2.0 mm. A subsample was taken for moisture determination and a second subsample was extracted with 2 *M* KCl using a 1:5 (w/v) extraction ratio (Keeney and Nelson, 1982). Samples were shaken for 2 h, centrifuged, and decanted to separate the soil from supernatant. Ammonium and nitrate concentrations of the extracts were determined colorimetrically (Adamsen et al., 1985) using a segmented flow autoanalyzer system (Alpkem Corp., Wilsonville, OR). Nitrate-N and NH_4–N were summed and are reported as mineral N.

In 1992–1993, plants were sampled for N concentrations from the 86 mm of row taken from above the root cores collected as described by Wechsung et al. (1999) on DOY 12, 32, 61, 90, 111, and 139, and in 1993–1994 on DOY 4, 25, 67, 102, 116, and 145 (Table 1). They were separated into leaves, stems, and heads and dried at 60°C, then weighed. Samples were analyzed for total N using an elemental analyzer (NA1500 Series 2, Carlo Erba Instruments, Rodano, Italy). All of the plant sampling dates were the same as those of Pinter et al. (1996) except for DOY 10 and 61 in 1993, which were DOY 12 and 62, respectively. For those dates, the aboveground biomass values were linearly interpolated between sampling dates to correct the values for the time offset. The N concentrations were then multiplied by the aboveground biomass values for each date to obtain the aboveground biomass N. In 1992–1993, weather and logistical problems resulted in differences of as much as 20 d in plant and soil sampling dates, but in 1993–1994 there was never more than 7 d difference between plant and soil sampling (Table 1).

Statistical analyses were performed using PROC GLM (General Linear Model Procedure) in SAS version 6.10 (SAS Inst., 1987). The main effect was split into a nonrandomized irrigation effect, which required the data to be analyzed as a strip-split plot design with four replications. In a strip-split plot design three error terms are used for statistical tests unlike a split plot design, which uses only two error terms. The error used for evaluating the main CO_2 effect was the $CO_2 \times$ rep interaction, the irrigation effect was tested using the irrigation $\times$ rep interaction, and the $CO_2 \times$ irrigation interaction was tested using the residual error, which in this case is the rep $\times$ CO_2 $\times$ irrigation interaction. Statistical differences and least square means comparisons were performed for sampling each date and soil depth. The $CO_2 \times$ irrigation interactions were not significant.

RESULTS AND DISCUSSION

Irrigation and CO_2 treatments did not result in large differences in soil N levels (Fig. 1 and 2). While differences were not statistically significant throughout most of the growing season, the levels of mineral N in the soil were the same or lower in the FACE plots than in the Ambient plots in almost all cases (Fig. 1 and 2).

Three Leaf Stage and Tillering

In 1992–1993, FACE plots tended to be lower in soil mineral N on the DOY 16 and DOY 23 sampling dates at all sampling depths (Fig. 1a, 1b). Day of year 16 and DOY 23 corresponded to three leaf stage and tillering, respectively (Table 1). Only a broadcast preplant application of fertilizer had been made before these dates (Fig. 3). The comparable plant sampling dates were DOY 12 and DOY 32, which was 13 d longer than the soil sampling interval. Aboveground biomass N in 1992–1993 was higher in the ambient plots (0.22 g m^{-2}) than in the FACE plots (0.19 g m^{-2}) on DOY 12, but by DOY 32 the difference was not significant (Fig. 4). Fertilizer N was applied on DOY 30, 2 d before the plant sampling, which may account for the difference in response to CO_2 between the soil and plant on the second sampling date. The concentration of N in the aboveground biomass decreased between the DOY 12 and DOY 32 (Fig. 5). The differences in N concentration of biomass among treatments within a sampling date were never significant.

In 1993–1994, the soil mineral N was lower on DOY 4 and DOY 32 than in the first two sampling dates in 1992–1993 (Fig. 1a, 1b, 2a, 2b, and 3; note scale difference between Fig. 1a and Fig. 2a). As in 1992–1993, the first two sampling dates for both soil and plants 1993–1994 corresponded to three-leaf stage and tillering. The differences in soil mineral N between FACE and ambient plots were similar in both years during the early part of the growing season. In 1993–1994, there were statistically significant CO_2 effects on soil N in the first two soil sampling dates (Fig. 2a, 2b). The aboveground biomass N content of the ambient plots was

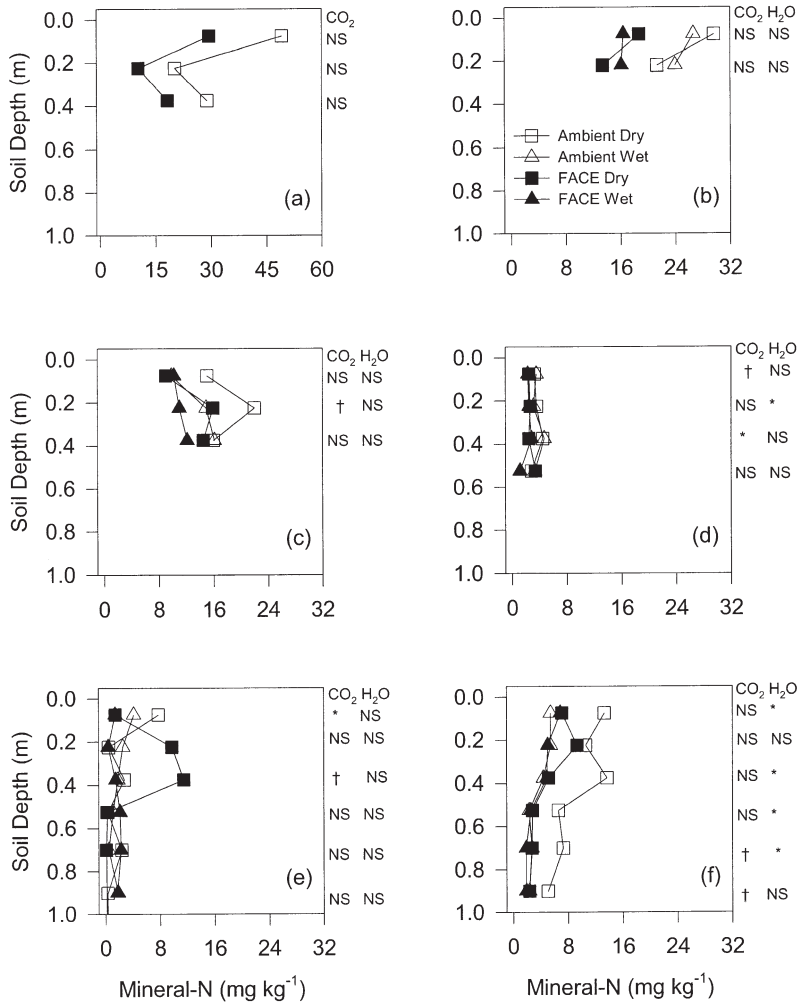

Fig. 1. Soil mineral N concentrations in the soil from FACE and ambient wheat plots in 1992–1993 at (a) day of year (DOY) 16, (b) DOY 23, (c) DOY 43, (d) DOY 70, (e) DOY 114, and (f) DOY 148. Shown also are main treatment effects for CO_2 and irrigation (H_2O) (NS, *, and † for not significant, $P < 0.05$, and $P < 0.1$, respectively).

higher than that of the FACE plots until DOY 67, stem elongation. Unlike 1992–1993, there was no fertilizer applied before the second plant sampling date on DOY 32. Wechsung et al. (1995, 1999) found that root dry mass was more than 20% higher in FACE plots than in ambient plots on DOY 4 and DOY 25. The more extensive root system of the FACE plants may account for the lower soil mineral N content on the first two soil sampling dates.

Stem Elongation

An application of fertilizer was made on DOY 30 in 1993 and DOY 34 in 1994 (Fig. 3), which was between the second and third soil sampling dates in both years (Table 1). The third sampling date corresponded to stem elongation. The drip irrigation system placed the fertilizer approximately 0.20 m below the soil surface. All sampling dates after the first fertilizer application in both years show a peak in the soil mineral N concentrations for one or more treatments between 0.3 and 0.5 m (Fig. 1 and 2). Soil mineral N concentrations were higher at stem elongation, which are the third points from the left in Fig. 3a and 3b, in 1992–1993 than 1993–1994. The fertilizer application was made 13 d before DOY 43 soil sampling date in 1992–1993 and 29 d before the DOY 63 in 1993–1994. The difference between years may reflect the difference in fertilization as well as the higher initial concentrations of soil mineral N in 1992–1993 than in 1993–1994 (Fig. 1a, 2a). At stem elongation, mineral N concentrations in the FACE plots were lower than those in the corresponding Ambient plots at all depths even though the CO_2 effect was significant at only one depth in each year (Fig. 1c, 2c). In 1992–1993, the plant samples were taken 18 d after the soil samples and in 1993–1994, plant samples were taken 4 d after the soil samples. Differences in the total aboveground biomass N on the third sampling date were small, not significant, and not consistent across years (Fig. 4). The concentration of N in the biomass continued to decline between the second and third plant sampling dates (Fig. 5). At the third plant sampling date, Wechsung et al. (1999) found that the root dry mass was 37% higher in the FACE treatment than the ambient treatment. The enhanced root system in the FACE treatments, which provided an increased ability to take up N, may

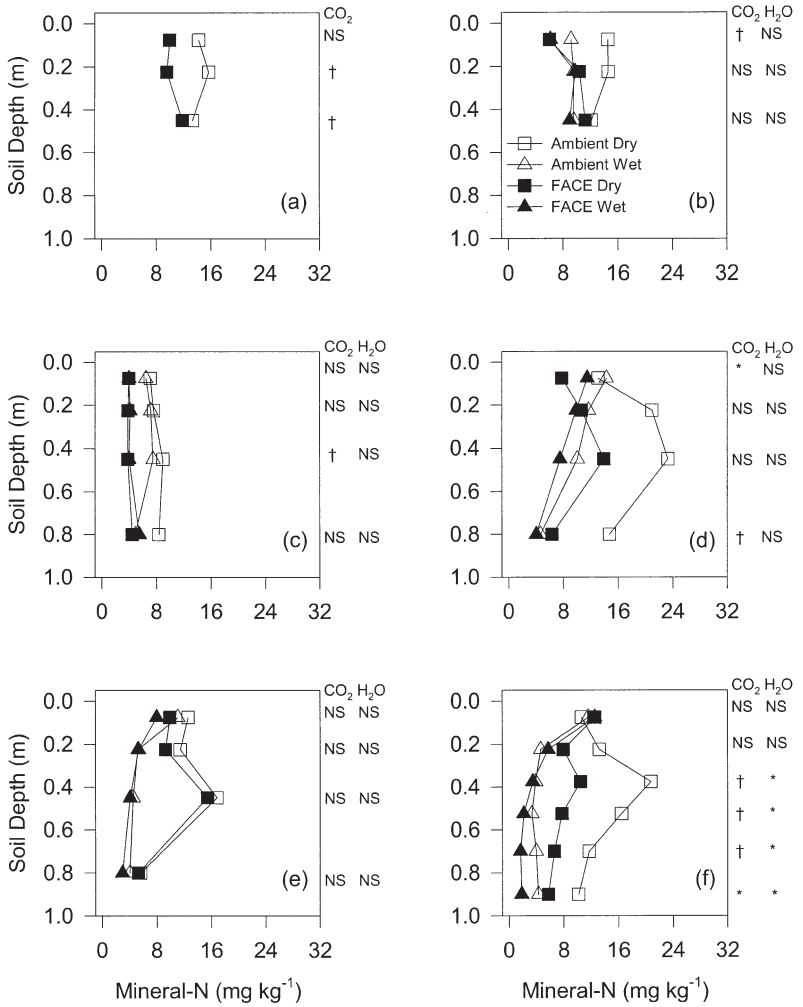

Fig. 2. Soil mineral N concentrations in the soil from FACE and ambient wheat plots in 1993–1994 at (a) day of year (DOY) 4, (b) DOY 32, (c) DOY 63, (d) DOY 103, (e) DOY 120, and (f) DOY 150. Shown also are main treatment effects for CO_2 and irrigation (H_2O) (NS, *, and † for not significant, $P < 0.05$, and $P < 0.1$, respectively).

explain the lower concentration of soil mineral N at some depths in the soil. The mineral N concentrations of the Wet treatments tended to be lower than the corresponding Dry treatments in both years, although differences were small and not significant (Fig. 1c, 2c). In previous studies, no differences were detected in soil water content or water use between the Wet and Dry treatments through stem elongation (Hunsaker et al., 1996) nor any differences found in aboveground biomass between wet and dry treatments (Pinter et al., 1996), which would also explain the lack of response of soil mineral N to irrigation treatment.

Early Milk Stage

The fourth soil sampling date was DOY 70 in 1993 and DOY 103 in 1994, which corresponded to boot and early milk, respectively (Table 1). In 1993, there were no fertilizer applications between the third soil sampling date on DOY 43 and the fourth soil sampling date on DOY 70. In 1994, there were two fertilizer applications between the third soil sampling date on DOY 63 and the fourth soil sampling date on DOY 103, the first on DOY 75 and the second on DOY 98. On the fourth soil sampling date in 1993, DOY 70, the concentration of soil mineral N was lower throughout the profile than on the fourth sampling date in 1994, DOY 103 (Fig. 1d, 2d), which was probably a result of the difference in time of soil samples and fertilizer application between the growing seasons. On the fourth soil sampling date, the plots in both FACE treatments were lower in mineral N than those from the comparable Ambient treatments in both years. There was a significant effect due to increased CO_2 on the mineral N of the surface layer in both years (Fig. 1d, 2d) as well as the total soil mineral N in the top 0.30 m of soil (Fig. 3). Soil mineral N in the top 0.30 m of soil was <2 g m^{-2} at early milk (Fig. 3a), which may have been low enough to cause some N stress during the 1992–1993 growing season. In 1993, the irrigation effect was significant for the 0.15- to 0.30-m depth on the DOY 70 soil sampling date, which may have been the result of redistribution of nitrate by irrigation water in the Wet treatments. Plant samples were taken on DOY 90 in 1993, 20 d later than soil samples, and DOY 102 in 1994, 1 d earlier than the soil

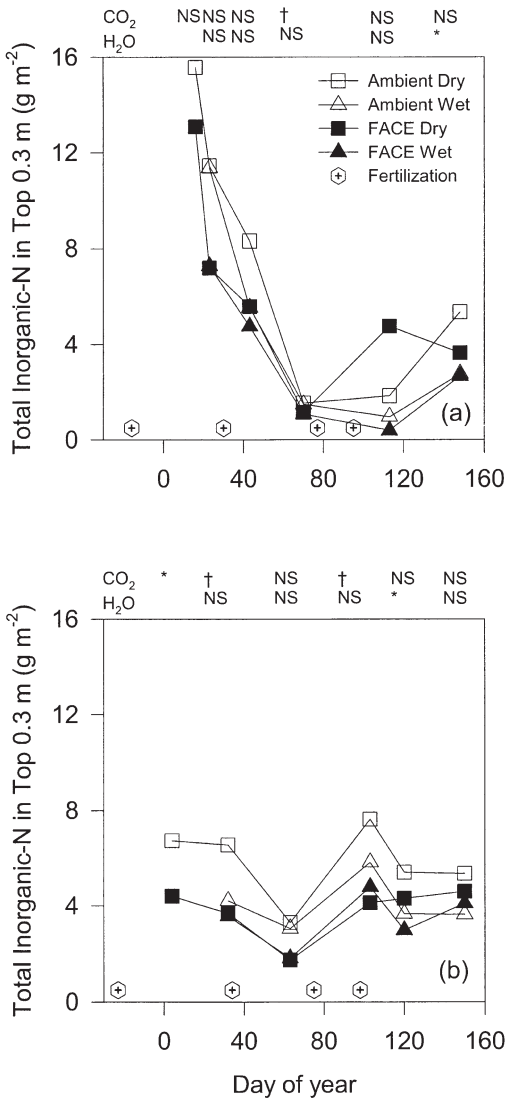

Fig. 3. Total soil mineral N in the top 0.30 m of soil from FACE and ambient wheat plots in (a) 1992–1993 and (b) 1993–1994. Shown also are main treatment effects for CO_2 and irrigation (H_2O) (NS, *, and † for not significant, $P < 0.05$, and $P < 0.1$, respectively).

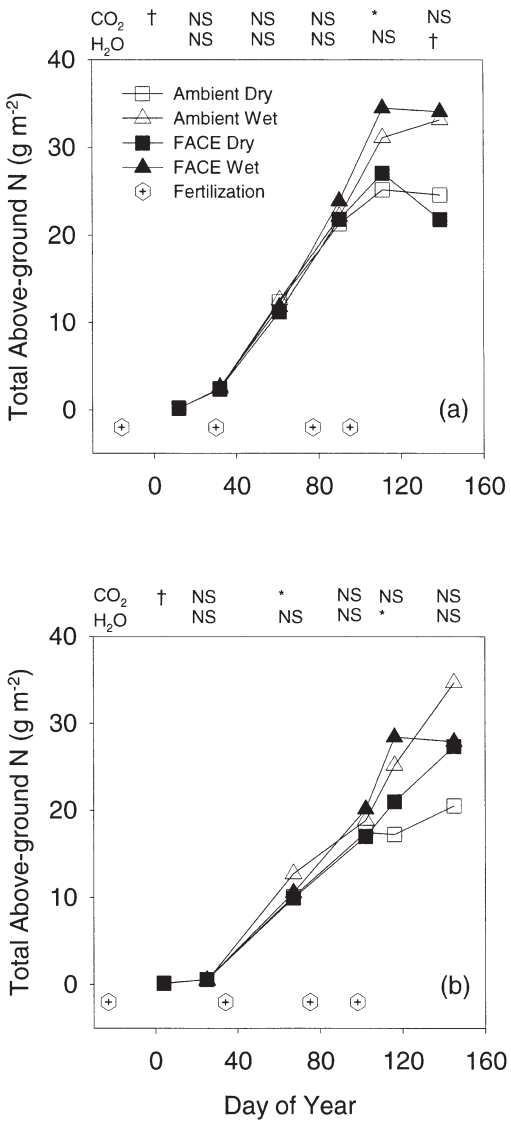

Fig. 4. Aboveground biomass N of FACE and ambient wheat plots in (a) 1992–1993 and (b) 1993–1994. Shown also are main treatment effects for CO_2 and irrigation (H_2O) (NS, *, and † for not significant, $P < 0.05$, and $P < 0.1$, respectively).

samples. The plant sampling date in both years was at early milk stage. There was one application of fertilizer between the third and fourth plant sampling dates in 1993 and two fertilizer applications in 1994 (Fig. 4). The aboveground biomass N was not different among treatments in either year on the fourth plant sampling (Fig. 4), and the amounts of N were comparable between years, even with the differences in timing of fertilizer applications between years. Wechsung et al. (1995, 1999) reported 7% higher root dry mass in the FACE treatments than in the ambient for the same sample dates, although the difference in root dry mass was not significant. Root growth appeared to be near its maximum at early milk (Wechsung et al., 1999).

Dough Stage

On DOY 113 in 1993, at the dough stage there was no clear trend in the soil mineral N concentrations (Fig. 1e), and on DOY 120 in 1993–1994, there were no differences in soil mineral N concentrations between treatments (Fig. 2e). Soil mineral N decreased in the top 0.30 m of soil between boot and dough stage in both years in all of the treatments except FACE Dry, even though there had been two fertilizer applications between the two sampling dates in 1992–1993 (Fig. 3a). In both years, there was an increase in the aboveground biomass N (Fig. 4) between early milk and the dough stage. Changes in both soil and plant N between the fourth and fifth sampling dates indicate uptake of N after anthesis. In 1993, CO_2 significantly affected the aboveground biomass N on the DOY 111 plant sampling date; in 1994, the irrigation effect was significant on the DOY 116 plant sampling date. Differences in evapotranspiration among treatments became significant between anthesis and dough stage (Hunsaker et al., 1996) as did accumulations in aboveground biomass (Pinter

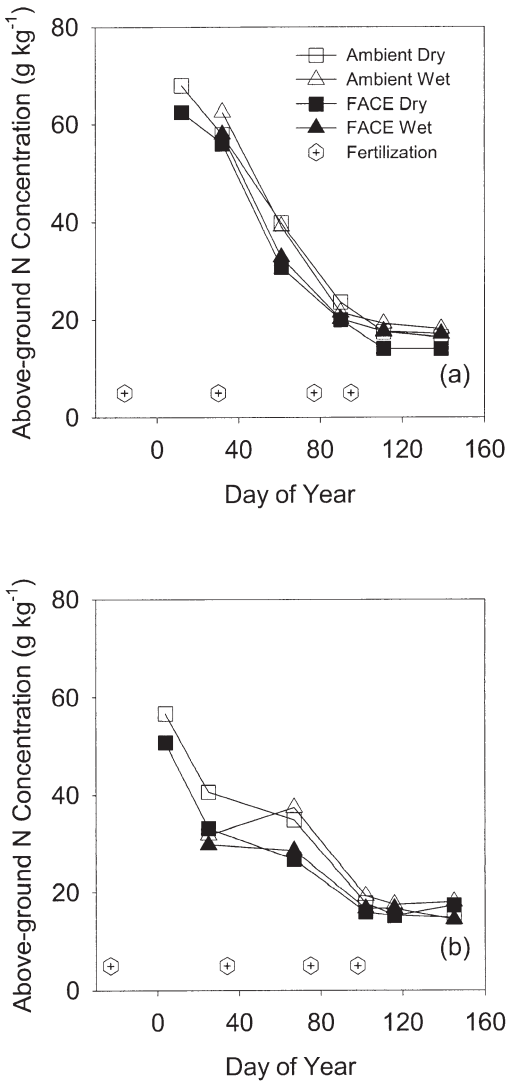

Fig. 5. Nitrogen concentration in the biomass of FACE and ambient wheat plots in (a) 1992–1993 and (b) 1993–1994.

et al., 1996), which corresponded to the differences in aboveground biomass N. In response to CO_2 and irrigation, aboveground biomass N tended to be lower in the Dry treatments in both years than in the Wet treatments and higher in FACE treatments than ambient treatments.

Final Harvest

By the final harvest soil sampling dates, which were DOY 148 in 1993 and DOY 150 in 1994, the soil mineral N concentrations of the Dry treatments were significantly higher than those of the Wet treatments at most depths (Fig. 1f, 2f). The mineral N content of the soil was higher in the top 0.3 m of soil in the Dry treatments than in the Wet treatments at final soil sampling date in 1993 but not in 1994 (Fig. 3). The last plant sampling dates, which corresponded to final harvest, were DOY 139 in 1993 and DOY 145 in 1994. At final harvest in both years, the aboveground biomass N was higher in the Wet treatments than in the Dry treatments, but the difference was significant only in 1993. During the period from dough stage to final harvest (Table 1), the effect of deficit irrigation reduced evapotranspiration (Hunsaker et al., 1996) and plant growth (Pinter et al., 1996), which also reduced demand for soil N. Root dry mass also declined in all treatments between dough stage and final harvest (Wechsung et al., 1995, 1999), which also reduced demand for soil N. In 1992–1993, the soil mineral N in the top 0.30 m of soil increased between the last two sampling dates for all treatments except FACE Dry (Fig. 3a), but remained unchanged in 1993–1994 (Fig. 3b). In 1993, the aboveground biomass N was either constant or dropped slightly between the last two plant sampling dates (Fig. 4a); in 1994, the aboveground biomass N increased in all treatments except FACE Wet during the same period. The increase in soil mineral N in the Dry plots between the last two soil sampling dates (Fig. 3) may indicate the start of decomposition of the root system of the maturing plants. Plants in the FACE plots also matured 4 d earlier than the ambient plots as a result of higher canopy temperatures, which sped up the development (Kimball et al., 1995; Pinter et al., 1996, 2000), but the small difference in development between FACE and ambient did not appear to be great enough to affect the soil mineral N.

The concentration of N in the aboveground biomass declined from 65 g kg^{-1} in 1992–1993 and 54 g kg^{-1} in 1993–1994 on the first plant sampling date at the three-leaf stage to 16 g kg^{-1} on the last plant sampling date at final harvest (Fig. 5). The trend on the first three plant sampling dates was for the plants from the FACE plot to have lower concentrations of N than those from the ambient plots in both years, which was consistent with the results reported by Cotrufo et al. (1998). At the last three plant sampling dates the differences between CO_2 treatments were smaller than those earlier in the growing season. The two N fertilizer applications made after DOY 70 in both years appear to have reduced the difference in N concentrations between the FACE and ambient plots. This suggests that fertilizer management can affect the composition of the aboveground plant material and reduce the effect of CO_2 on plant N concentrations.

CONCLUSIONS

In both years of the study, soil mineral N levels tended to be lower in plots that were exposed to elevated CO_2 (FACE), but the differences were small and not statistically significant until near the end of the growing season. After anthesis (~DOY 80 in 1993 and ~DOY 90 in 1994) in plots that received deficit irrigation, soil mineral N levels tended to be higher than in those plots receiving adequate irrigation. Total aboveground biomass N tended to be higher, but not significant in plots that were exposed to elevated CO_2 than in the ambient plots. The trajectory of the aboveground biomass N through the growing season was reversed from that of the soil mineral N in the top 0.3 m of the soil, suggesting that aboveground biomass N could account for at least some of the seasonal change in soil mineral N. However, the large increase in root dry mass in plots exposed to ele-

vated CO_2 probably had a greater affect on the soil mineral N.

Aboveground biomass N tended to be lower in deficit irrigated plots after anthesis than in those which received adequate irrigation. Irrigation did not affect soil mineral N until after anthesis, which was consistent with differences in evapotranspiration (Hunsaker et al., 1996) and total biomass (Pinter et al., 1996) in either year of the study.

Application of N fertilizer through the subsurface drip irrigation system used in this study affected the distribution of soil mineral N in the profile. After the first application of fertilizer through the irrigation system, there was always a peak in the N concentration of the soil between 0.3 and 0.5 m below the soil surface.

Under the conditions of adequate N used in this study, the levels of N in the aboveground biomass did not vary widely between treatments. The concentration of N in the biomass tended to be lower under elevated CO_2 than under ambient conditions before the last two N applications, which were after boot stage, but the differences were much smaller after the last two fertilizer applications. This was consistent with previous work (Sinclair et al., 2000) that the forage quality and raw protein levels in leaf tissue was not affected by CO_2 or irrigation in this study.

Elevated CO_2 did not result in major differences in either aboveground or belowground N in this field study where N fertility was adequate. However, the differences that did emerge suggest that under field conditions plants grown under elevated CO_2 have the potential to take up soil N more rapidly than plants grown under ambient conditions. Rapid uptake of N early in the growing season could lead to vegetative growth that has been shown to reduce grain yields (Cure et al., 1988; Goudriaan and de Ruiter, 1983; Israel et al., 1990). More field research is needed to determine how elevated CO_2 may affect fertility management of wheat and the effect of low fertility under elevated CO_2 on wheat.

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